THE ANATOMY AND TAXONOMY
OF *INDOSTOMUS PARADOXUS*
PRASHAD & MUKERJI

BY

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ABSTRACT

The osteology of *Indostomus paradoxus* Prashad and Mukerji is described and the evidence for its affinities discussed. The array of characters common to both *Indostomus* and the higher paracanthopterygii suggests a relationship between the two groups which is expressed by proposing a new paracanthopterygian order—Indostomiformes—of which the only known representative is *Indostomus paradoxus*.

INTRODUCTION

Indostomus paradoxus was discovered by the Indian Museum Expedition of 1926 in Lake Indawgyi, a large shallow lake in the Myitkyina district of Upper Burma. The series of specimens collected (about 30) was named and briefly described by Prashad and Mukerji (1929). Most of the specimens were housed in the Indian Zoological Survey in Calcutta, except for five which were presented to the British Museum (Natural History) and at least one was presented to the United States National Museum.

Bolin (1936) briefly redescribed the U.S. National Museum specimen but the unavailability of further specimens resulted in the only two descriptions of this species being superficial.

Materials and Methods

One of the five specimens at the B.M. (N.H.) [No. 1937.9.25 : 1–5] had been prepared by the alizarin method but was not suitable for detailed examination. I was, therefore, delighted to receive another specimen from Dr. Earl Herald of the Steinhart Aquarium, California Academy of Sciences (CAS-ACC 1963–xii–16). This fish was one of six which arrived at an aquarium fish importers in America and was described as having come from " Mountain streams remote from Bangkok ". Doubt has since been cast on this locality (Herald pers. comm.). I prepared this fish by the alizarin method and dissected it.

Since then I have obtained about 140 specimens from Dr. Alan Tubb of the F.A.O. in Thailand. Dr. Tubb collected them from a stream at the west side of Lake Indawgyi in 1956, kept them alive in Aquaria and made invaluable notes on their behaviour (see Appendix 1). It is with great pleasure that I acknowledge his kindness in making both his notes and specimens available to me.

Some of the specimens have been stained with alizarin and dissected as before. I have also had prepared longitudinal and transverse serial sections, stained in Mallory's triple stain. Other specimens have been presented to various museums throughout the world.

The size range of the specimens was 21–27 mm. (standard length). The line drawings of the bones were made from different specimens but all were within the 24–27 mm. s.l. range.

Terminology

The bone terminology generally follows Harrington (1955) although with only adult specimens available I cannot be too certain about the dual origin of some bones ; in these cases the dermo- and auto-prefixes will not be used. The terms dentary, angular and articular are retained for the three bones of the lower jaw. I fully accept the inaccuracies implied in this but it is a convenient labelling system (Weitzman 1962), especially in the absence of embryological information.

Nelson (1967) has been followed for the naming of the pharyngeal bones.

Greenwood *et alii* (1966) have been followed for classification above the genus level. The names given to the muscles are merely indicative of their position and

function ; identity with muscles of the same name in other fishes is not necessarily intended.

THE OSTEOLOGY OF *INDOSTOMUS PARADOXUS*

The body of *Indostomus* is very slender, slightly depressed and covered in scutes (fig. 1). The presence of this dermal armour has had a modifying effect upon the axial skeleton and musculature.
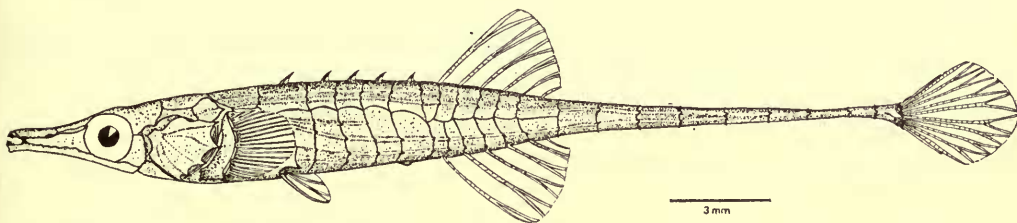

FIG. 1. *Indostomus paradoxus* Prashad and Mukerji. Lateral view.

Body Armour

In the abdominal region there is a median row of dorsal plates and two rows of ventrolateral plates. The latter irregularly overlap in the ventral midline and their dorsal edges overlap the ventral margins of the dorsal plates. In front of the last dorsal fin ray the dorsal plates are convex, behind it they are flat. The plates are also flattened on the ventral surface of the abdomen.

There are twenty-one dorsal plates (rarely twenty) corresponding in number, but not always in position, to the vertebrae. The first plate is loosely connected to the head by a fold of skin which allows the fish to move its head (see Appendix 1). Each of the next five plates (Nos. 2 to 6 inc.) bears at its centre a small mobile spine which supports a flap of tissue. The depression in which each spine articulates is perforated by a pair of tendons attached to the muscles fastened on to the median keel of the plates. The articulation mechanism of one of the spines is shown in fig. 2.
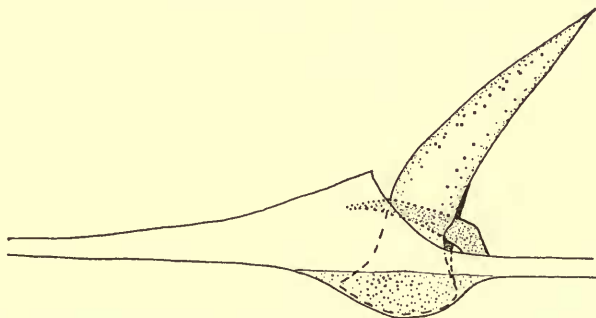

FIG. 2. Diagram of the articulation of one of the dorsal spines.

The first ventrolateral plate has been incorporated into the pectoral fin skeleton (see below). The anteroventral margin of the second has been expanded forwards and lies below the pectoral fin. A notch in its posterior margin marks the position of

the articulation of the pelvic fin, which is on the third plate (fig. 1). The first five
dorsal and anal fin rays articulate between the plates ; the sixth, like the isolated
dorsal spines, is in the centre of the plate. Posterior to the median fins the plates
become fused to give the body a quadrangular cross section. A series of cristae run
along the length of the body ; towards the caudal region they coalesce and emphasize
the rectangular cross section of the caudal region.

Vertebral column

There are 21 (rarely 20) vertebrae, of which nine are abdominal. Transverse
processes, which originate at the base of the anterior part of the neural arch, are
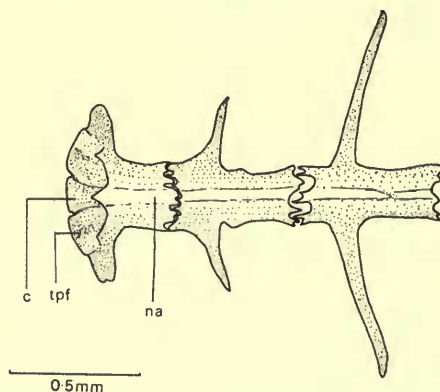present on vertebrae 2–9 inclusive (figs. 3 and 4). Ribs are absent.

c   tpf   na

0·5mm

Fɪɢ. 3.   Dorsal view of the first three vertebrae.   For explanation of the abbreviations
see key on page 207.

The first vertebra (figs. 3, 4, and 12) is modified to allow for the depression and
elevation of the head (see Appendix 1). The transverse processes are broad and
arise from the centrum. A part of the leading edge of each transverse process is
extended forward as a shallow socket to receive the exoccipital process dorsally
(figs. 4 and 12). The neural arch of the first vertebra is fused to the centrum and has
a sloping anterior face to permit the elevation of the head. This elevation is effected
by the contraction of epaxial muscles which are connected to the epiotics by ossified
tendons. I am unable to explain the mechanism which causes the lateral flexures of
the head noticed by Dr. Tubb (see Appendix 1).

The transverse processes on the abdominal vertebrae do not contact the dermal
plates. The neural arches of the abdominal vertebra (fig. 4) have a complex inter-
digitation with each other ; neural spines are not formed.

The last abdominal vertebra (the ninth) has short, thin transverse processes and
the posterolateral edges of the centrum develop as small wings which articulate with
the front edges of the haemal arch of the tenth vertebra. Vertebrae 11–21 (or 20)
have neural and haemal arches which become progressively shallower and after the
fourteenth vertebra fuse with the dermal armour so that the nature of the neural
spine of the last caudal vertebra cannot be determined.

A series of ossified tendons lies horizontally in the axial musculature. Some originate on the ventral keels of the dorsal row of plates, others originate in the musculature, but all run caudally to transmit the contractions of the anterior muscles to the posterior part of the body. A cross section of one segment of the caudal
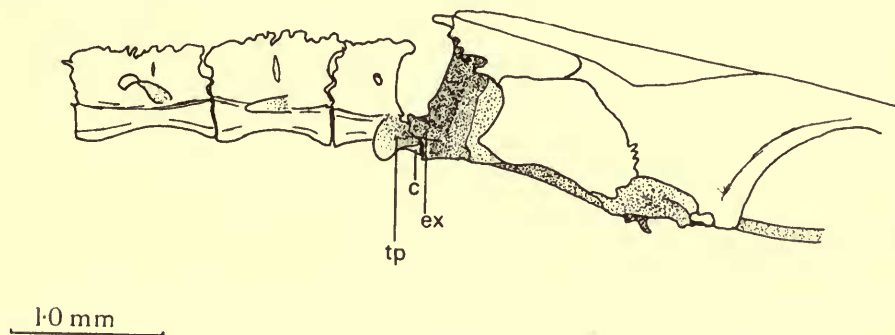
FIG. 4. Lateral view of braincase and anterior vertebrae to show the occipital articulation.

region reveals an external ring of armour divided vertically by the vertebra, with four groups of tendons ; situated above and below the centrum on each side. Very little musculature is present.

Caudal fin

The caudal fin is large and fan-shaped (fig. 1). It is dorsoventrally symmetrical and in each half there are two small procurrent rays, one principal unbranched ray and four or five branched rays (figs. 1 and 5).
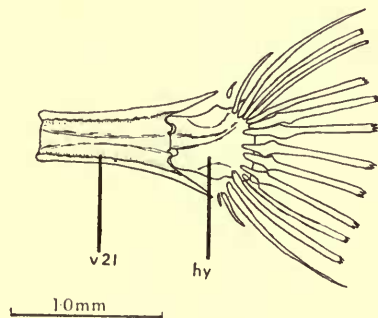
FIG. 5. Caudal fin skeleton.

The caudal skeleton consists of a preural centrum fused with the hypurals into a single solid unit. It is extremely small and no evidence of any fusion of parts is available.

Median fins and their skeletal supports

The isolated dorsal spines which may represent the first dorsal fin have been mentioned above. The median keels of the dorsal plates (fig. 6) appear to fulfil the

function of proximal radials for all the median fin rays. The dorsal and anal fins both have six segmented rays, all but the last being branched. Differences in the position of branched and unbranched rays relative to the scutes has been commented on above (and see fig. 1). A small nodule of cartilage (the distal radial?) is found between the bases of the lateral halves of each fin ray.
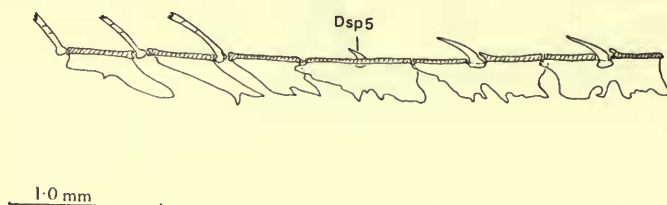
FIG. 6. Diagram of the last three dorsal spines and the first three dorsal fin rays to show the fin supports. The fifth spine is out of alignment.

Pectoral fin skeleton

The pectoral fin has 23 rays, of which 15 are segmented. The supracleithrum (fig. 7) is lodged ventrally in a niche on the first lateral scute which has been incorporated into the pectoral skeleton. Functionally, the cleithrum is represented by this first scute and the median flange on its anterior edge, but it is probable that the flange alone represents the cleithrum which has fused with the scute. The outer part is ornamented in the same way as the other scutes and is clearly in series with
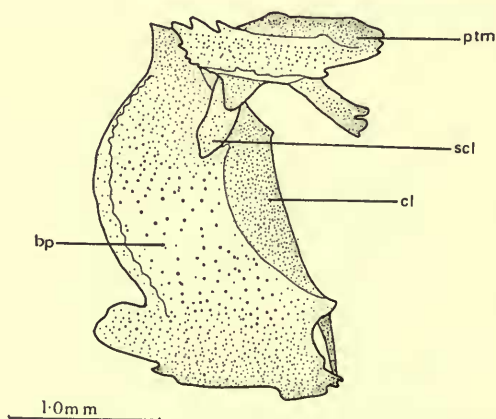
FIG. 7. Lateral view of the dermal elements of the pectoral fin skeleton.

them. Only the flange forming the hind wall of the gill chamber really distinguishes it. I hesitate to refer to the scute-like part of this bone as an infracleithrum (Swinnerton 1905) which is a similar bone in *Gasterosteus*, because of the position of the supracleithrum. Applying Occam's razor the most likely explanation is the fusion of the cleithrum and the scute. The cleithra interdigitate in the midventral line.

The endochondral part of the pectoral skeleton consists of a coracoid, a scapula and three pterygials (fig. 8).   Baudelot's ligament is absent.
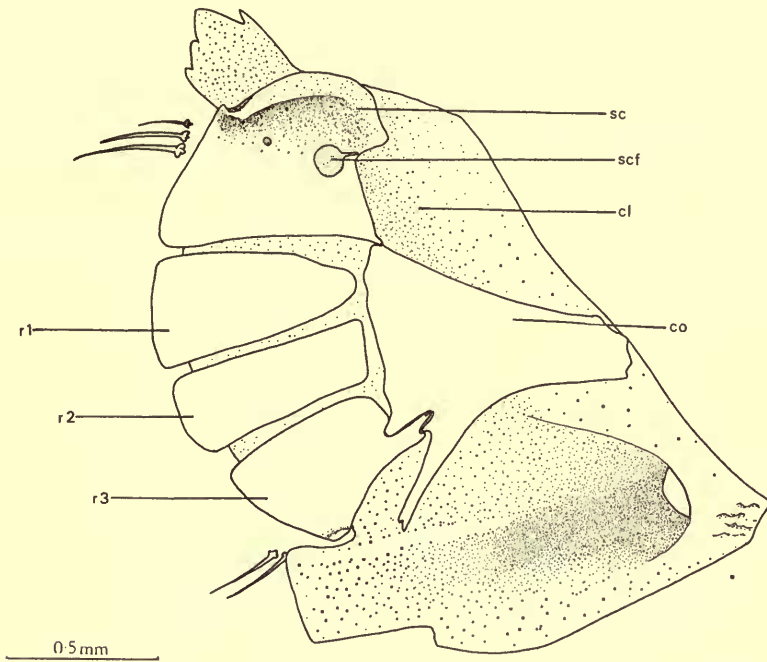
FIG. 8.   Medial view of the pectoral fin skeleton.   Only the upper and lower pectoral fin rays have been drawn in.

The coracoid has a posteroventral process which rests on the cleithrum.   The scapular foramen is contained entirely within the scapula and only just fails to open anteriorly.   The dorsal margin of the scapula is expanded horizontally, and laterally it fits closely on to the dorsal edge of the scute.   The recess below the dorsal lip of the scapula on its median face houses the origin of muscles which run to the pectoral fin.   The coracoid, scapula and pterygial ossifications are all contained within a sheet of cartilage and are joined to each other more firmly than they are to the rest of the pectoral skeleton.   There is a possibility that the scapula has fused with the uppermost pectoral pterygial.   This has happened in other fishes eg. *Scorpaenichthys* (Starks 1930) and would account for the low number of pterygials.

Pelvic fin and skeleton
    The pelvic fin consists of four segmented rays.   The outermost ray is thickened, and the middle two branched.   The base of the fin articulates on a small boss in the centre of a depression near the rear margin of the second ventrolateral scute (fig. 1). Rays 2, 3 and 4 share either one elongated or two small rounded ossicles lying between their divided bases.   The first ray is not so markedly bifurcated at the base and articulates directly with the boss.

B

The pelvic girdle is reduced to a small ridge of bone in the medial face of the scute.

SYNCRANIUM

The skull is fairly flat on top and rather depressed. The dermal bones are pitted and ridged, with most of their edges crenellated or spiny. A series of ridges on the skull (figs. 9 and 10) suggest the presence of an extensive cephalic lateral line system, but close examination of sections has shown that in all probability the lateral line system is confined to a pair of short tubes between and slightly in front of the orbits (see below).

The eyes are large, the snout moderately elongated and the mouth is small and terminal. The most remarkable feature of the mouth is the great discrepancy between the lengths of the upper and lower jaws (fig. 9).
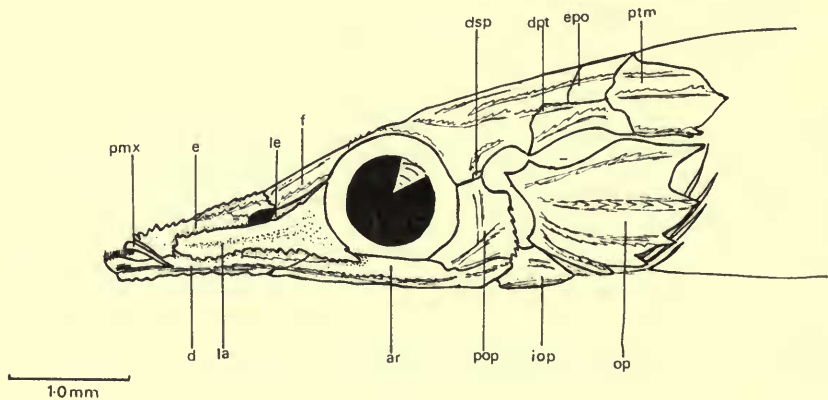
FIG. 9.   Head of an unprepared specimen in lateral view.   The ridges are illustrated diagramatically.

Olfactory region

The bones present are the ethmoid, lateral ethmoids, supraethmoid and vomer. The nasal bone is absent.

The ethmoid and the supraethmoid are fused together to form one functional unit with the supraethmoid as a dorsal shield over the wedge shaped and largely cartilaginous ethmoid (figs. 10 and 11).

On a few specimens up to four small pits are present near the anterolateral corners of the dorsal surface of the supraethmoid.

The leading edge of the ethmoid block is formed entirely from the supraethmoid and the maxillae and premaxillae are bound to it by fibrous tissue. The anterior nostril (fig. 10 anf) has a flap of skin which directs the water over the olfactory organ and into the canal between the lachrymal and the ethmoid. For most of its length the canal is roofed by the dorsal edges of the supraethmoid and lachrymal which are joined by collagen fibres. The anterior nostril is floored by a process from the ethmoid block which has a ligament joining it to the lachrymal.

The lateral faces of the ethmoid are produced ventrally as sheets for the attachment of the pterygoquadrate arch.

The vomer appears to have fused so firmly with the ventral face of the ethmoid that prolonged maceration will not separate them. Serial transverse sections show that there is no line of weakness nor any sign of a joint between the vomer and the ethmoid. There are two possible explanations for this, but no conclusions can be
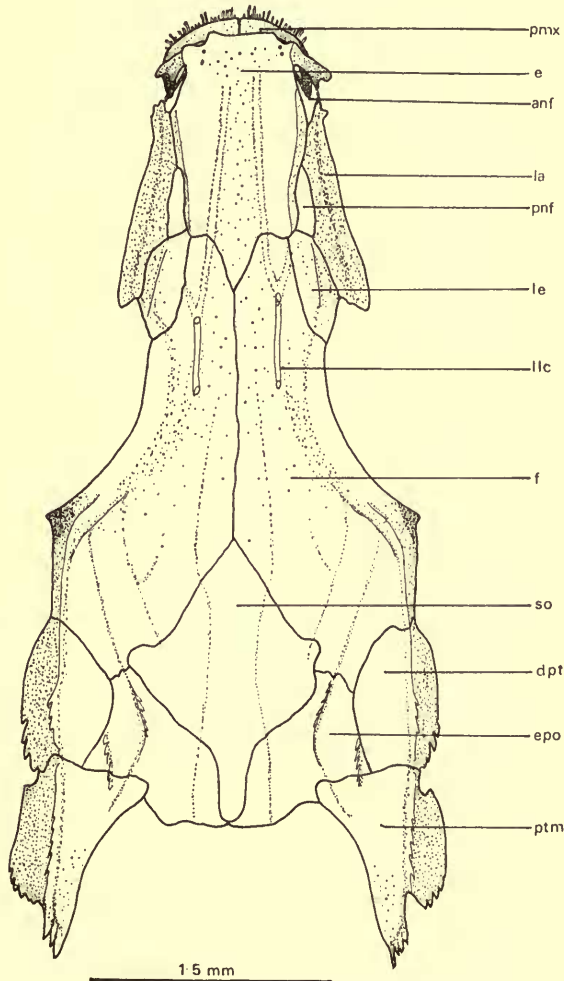
FIG. 10. Dorsal surface of the skull.

reached without an examination of much younger fishes than I have been able to obtain. Either there is no vomer, and its place has been occupied by a posterior projection from the ethmoid, or the ethmoid and vomer have co-ossified.

For convenience the process in question will be referred to as vomer. It is toothless and has the usual relationships of a vomer bone, except at its anterior end (fig. 11).

The lateral ethmoid (figs. 9, 10, 11) forms the hind margin of the posterior nostril.

Little of this bone is visible in lateral view (fig. 9).   The ventral face is concave with the median wall more or less contiguous with the expanded lateral edge of the ethmoid bone.   The parasphenoid separates the lateral ethmoids in the midline.   The portion of this bone which is visible externally is sculptured, so presumably a prefrontal bone is present as well.
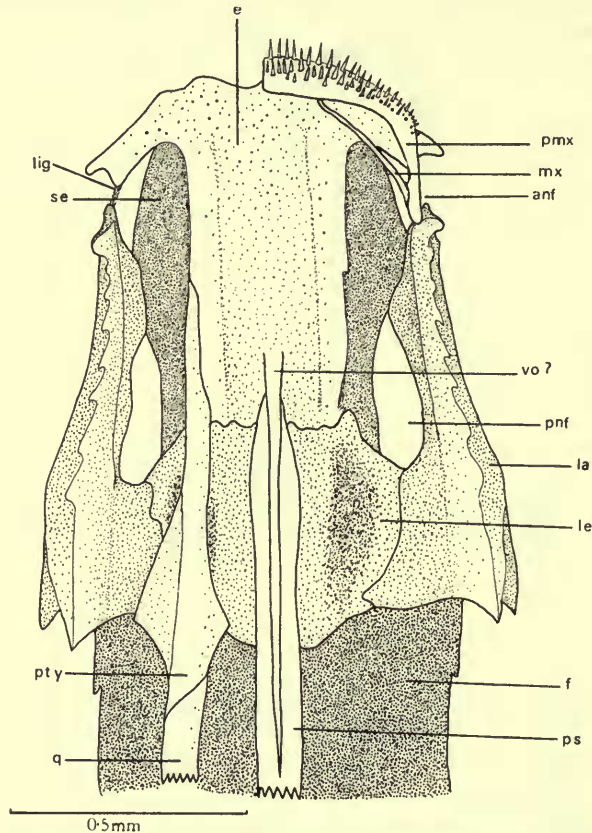
Fig. 11.   Ventral surface of the snout.   The left pterygoid bar and the right maxilla and premaxilla have been removed.

Orbital Region

The small tubes containing the lateral line canals in the frontals vary in length in different specimens.   This is an indication that the cephalic lateral line system has undergone reduction.   Small descending frontal processes are present (fig. 12) which form a groove with the lateral, post-orbital part of the frontal.   This groove is blocked posteriorly by the sphenotic, and houses what appears to be a part of the muscle block associated with the operculum, although I hesitate to refer to them as dilatator operculi muscles as they are highly modified and also seem to insert on to the preoperculum.   The frontals meet in the midline by a series of irregular overlaps.

The pterosphenoids are axehead-shaped bones which just meet each other in the

ventral midline above the parasphenoid (fig. 12). The posterior edge of each bone contributes to the margin of the anterior foramen of the pars jugularis of the tri-gemino-facialis chamber.
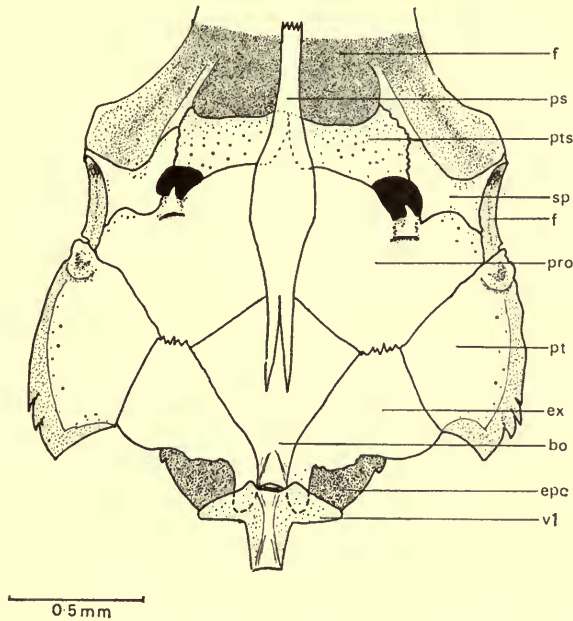
FIG. 12. Ventral surface of the braincase and first vertebra.

The sphenotic is a bone of complex shape, the main part of which resembles a con-vex cap forming the anteroventral corner of the neurocranium. It forms the lateral margin of the anterior trigemino-facialis foramen (fig. 12). A thin, laterally directed process is present which appears on the external surface of the skull, with the frontal, just behind the orbit (figs. 9, 12). The extremity of this process is expanded and sculptured and may well represent a dermosphenotic. It has been labelled as such in fig. 9.

The parasphenoid penetrates deeply into the cartilage of the ethmoid, and is held in place anteriorly by collagen fibres. Ascending processes are absent and the bone is slightly flattened between the eyes. A thin sheet of muscles originates on the orbital part of the parasphenoid and inserts on the " pterygoid ", this seems to be the adductor arcus palatini.

Only one infraorbital bone is present and that is the lachrymal (figs. 9, 10, 11). The anterior extremity of the lachrymal is joined by a ligament to the ethmoid. The lachrymal forms the outer wall of the olfactory cavity. An examination of the ol-factory region reveals the presence of a few strands of tissue which Dr. L. Bannister of Guys Hospital has suggested may well be the remains of a plunger mechanism. The preservation of the fishes is unfortunately not good enough to comment further on this. The plunger (if that is what is it) lies behind the nasal epithelium close to the anterior nostril.

Otic and Occipital Regions

Each prootic is separated from its partner in the midline by the parasphenoid (fig. 12). The distal wall of the trigemino-facialis chamber is thickened and produced anteriorly as a small spike below the anterior foramen for the chamber. From this projection collagenous fibres insert on to the inner face of the hyomandibular. The trigemino-facialis chamber is reduced, the medial wall is missing and only two external foramina are present (fig. 12).

The bone labelled epiotic in fig. 10 appears to have a dermal component which may represent a parietal ossification which has fused with the epiotic. The posterior edge is smooth and is overlain by the first dorsal scute. Two pairs of ossified tendons from the axial muscles insert on this region (see above). A shallow post-temporal fossa is present, floored by the epiotic and pterotic.

Both the dermal and the endochondral parts of the pterotic are present. They can be described as two flat plates meeting at an angle at the lateral edge of the skull with the dermal plate overhanging the endochondral plate (fig. 12). At the widely separated medial edges of the plates, two vertical struts of endochondral bone create a chamber which has three openings. The posterior foramen opens into a cavity on the inner surface of the prootic and the small anterior foramen opens close to the hyomandibular socket. This cavity must largely house the inner ear but there is no trace of otoliths in either whole specimens or in the sections.

The ventromedial corner of the exoccipital is produced backwards, slightly beyond and level with the midpoint of the basioccipital condyle to articulate with the modified transverse processes of the first vertebra (figs. 3, 4, 12). A small pit is present on the posterior wall of the bone in which the descending process of the post-temporal lodges. The foramen magnum is tube-like, and formed mostly from the exoccipitals which just meet dorsally below the supraoccipital. The latter bone has a sculptured surface; there is no occipital crest, just a flat plate narrowly separating the epiotics (fig. 10).

The basioccipital has a convex condyle which does not protrude as far as the exoccipital condyles.

The posttemporal overlies the rear margins of the epiotic and pterotic. The serrated, sculptured dorsal plate is slightly convex (figs. 7 and 10) and from the underside of this there are two processes. The larger central process (fig. 7) abuts onto the exoccipital and the small process has the supracleithrum adhering to its medial face. The supracleithrum does not extend above the cleithrum.

Oromandibular region

The premaxillae are expanded at the symphysis and bear about four rows of fine pointed teeth (fig. 11). The symphysis is weak, the usual jaw ligaments are missing and the upper jaw bones are contained within the fibrous tissue of the upper "lip". Ascending processes are absent (fig. 10).

The maxilla is a greatly reduced, weak bone (fig. 11). Its posterior end is expanded slightly and it is very firmly attached to the dorsal edge of the premaxilla. The length of the maxilla varies from specimen to specimen, in some it almost

reaches to the midline. A discussion of the jaw mechanism will be found below. (page 196).

The angular is a small bone, more easily seen in sections than in gross dissection, which lies in a deep pit on the posterior margin of the articular (fig. 13). The articular is greatly elongated and occupies over three quarters of the length of the lower jaw (fig. 13). The lateral face is sculptured and a ridge marking the position of Meckel's cartilage is visible. The tendon from the adductor mandibulae muscles inserts onto the dorsal margin in a gutter formed by the development of a medial shelf below the eye. The anterior end of Meckel's cartilage is medially grooved and receives the posterior projection of the dentary.

A small coronoid process is present near the posterior end of the dentary (fig. 13). The symphysial region is expanded as a dentigerous plate which extends in front of the premaxillary tooth plate so that occlusion only occurs on the posterior half of the former plate.

The seamoid articular is a small, roughly cylindrical bone (fig. 13) in close proximity to the ectosteal part of the articular. It lies in the tendon at the ventral end of the adductor mandibulae muscles which are in an unusual position as a result of the elongation of the mandible (see below).
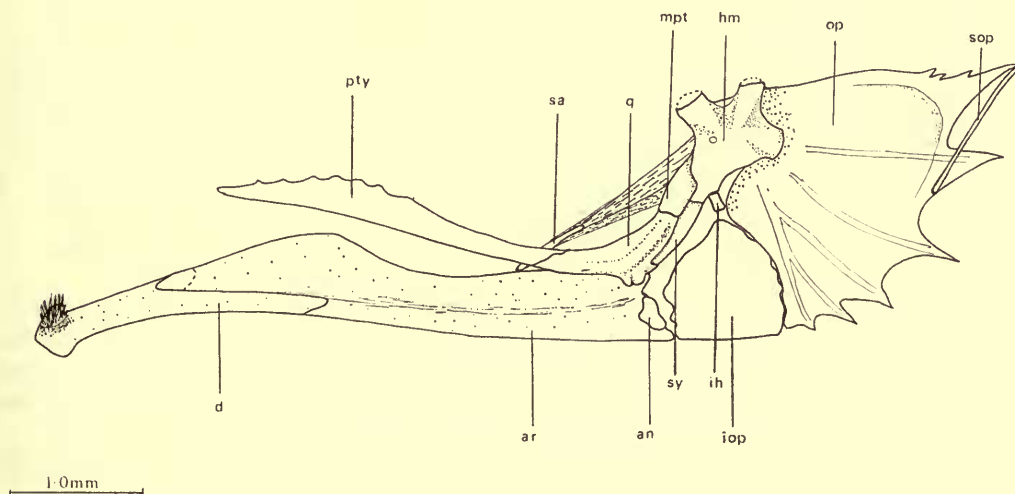
FIG. 13. Medial aspect of the suspensorium, opercular bones and mandible. Part of the medial adductor muscle has been removed to show the sesamoid articular.

Palatoquadrate arch

The palatoquadrate arch lacks the usual complement of bones (fig. 13). One long bone, the " pterygoid ", fills the places usually occupied by the ectopterygoid, endopterygoid and palatine. There is no indication of separate centres of ossification in the adult fish so the real identity of the bone must remain hidden until young stages can be found. In *Gasterosteus* there is a large tri-radiate " pterygoid " bone formed by the fusion of the ectopterygoid and endopterygoid. In the syngnathids the endo-

pterygoid is the largest element whilst in the triacanthid fishes neither the ecto-pterygoid nor endopterygoid is greatly enlarged. Therefore, just because jaw or snout elongation has occurred, it cannot be stated that certain pterygoid elements necessarily enlarge, fuse or disappear.

If the vomer has co-ossified with the ethmoid block (see page 189) then there are slight grounds for offering the suggestion that the descending sheets on the ventral face of the ethmoid represent anterior suspensorial bones (probably the autopala-tines) fused with the ethmoid as an added strengthening member. This must remain conjectural however until the ontogeny is known.

The " pterygoid " is largely a thin lath of bone with the dorsal margin below the eye bent over laterally to conform to the curvature of, and to support, the eye. In front of this, a dorsal lamella develops at an angle to the rest of the bone to form the groove which will anteriorly hold the descending sheets from the ethmoid (fig. 11). At the widest part of the pterygoid, just at the front of the orbit, a ligament joins it to the lachrymal.

The quadrate has an elongated lower limb (fig. 13), with the articular condyle as a transverse cylinder placed ventromedially—dorsolaterally at its heel. The dorsal limb is shorter than the ventral limb but extends further on the medial side where it overlaps the metapterygoid. The posterior edge of the quadrate is channelled to receive the symplectic.

The metapterygoid dorsally articulates with the hyomandibular, and the ventral part of its posterior margin contacts the symplectic. Both the metapterygoid and the dorsal blade of the quadrate are angled more towards the midline than is the rest of the suspensorium. The symplectic is a thin conical bone which is housed in a groove on the rear edge of the quadrate (fig. 13). It is poorly ossified and has a synchondrosis with the hyomandibular.

Opercular series

The operculum is armed with six conspicuous spines (fig. 13). The hyomandibular socket faces forwards at the anterodorsal edge of the bone. Medially, the posterior margin bears a shelf underneath which the levator operculi muscles from the hyo-mandibular insert. The dilatator operculi muscles insert on the anterior projection of the operculum in front of the hyomandibular socket.

The suboperculum is greatly reduced to a thin rod inside the posterior margin of the operculum (fig. 13).

The interoperculum is a flat sculptured bone connected to the mandible by a short but ill-defined interoperculo-mandibulare ligament. A loose interdigitation exists between the interoperculum and the operculum.

The preoperculum has a firm ligamentous connection to the quadrate along its ventral edge. The greatest expansion of the adductor mandibulae muscles occurs in the space between the preoperculum and the suspensorium.

Hyoid arch

The interhyal is a flat quadrangular bone with its dorsal margin fitting into a trans-verse groove in the posterior face of the hyomandibular (fig. 13).

The epihyal and ceratohyal are ankylosed dorsally and both have a depressed section (fig. 14). There is no foramen in the ceratohyal. Two slender branchio-stegal rays articulate on the lateral face of the slender part of the ceratohyal and two
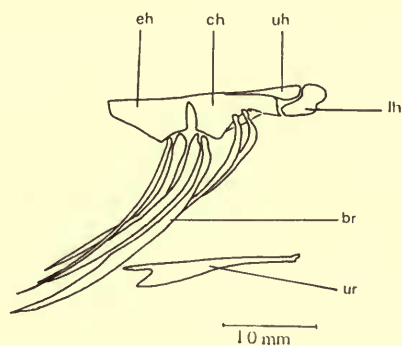

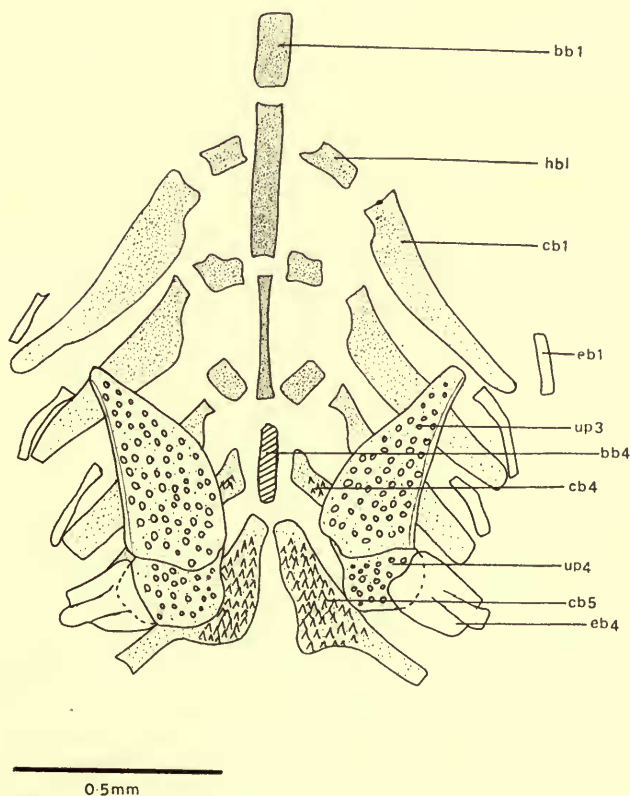FIG. 14. Lateral aspect of the hyoid bar, branchiostegal rays and urohyal.

FIG. 15. Dorsal view of the pharyngeal skeleton. Basibranchial 4 is cartilaginous.

thicker rays articulate on the same face of the expanded part. One thick and one thin branchiostegal ray articulate on the epihyal (fig. 14).

The upper hypohyal is a splint-like bone lying along the dorsal face of the cerato-hyal to meet the lower hypohyal (fig. 14).

The basihyal is a flat bone about four times as long as it is wide. The urohyal (fig. 14) is keeled and the posterior half of the bone is protected ventrally by a triangular median dermal plate which lies in front of the first ventrolateral body plates.

The hyomandibular (fig. 13) is a roughly cuboidal bone with the foramen for the hyomandibular nerve below the anterior articular head. The sockets on the neuro-cranium for the hyomandibular are shown in fig. 12.

Branchial skeleton

Ceratobranchials 4 and 5 have fused with tooth plates. Those on the fifth cera-branchials are the larger but they do not meet in the mid-line (fig. 15).

The fourth epibranchial is expanded and lies above the fourth upper pharygeal tooth plate. The larger anterior pharyngeal tooth plate is probably the result of the fusion of the second and third toothplates with the second and third infrapharyngo-branchials, the latter being represented by a thickening of poorly ossified endochon-dral bone along the lateral edge of the plate. There is no trace of the fourth infra-pharyngobranchial.

There are three irregularly cuboidal hypobranchials. The fourth basibranchial is distinct but does not ossify.

NOTES ON THE SOFT ANATOMY

I. The jaw mechanism of *Indostomus*

The upper jaw cannot be protruded, the maxillae and premaxillae are bound to each other and to the front of the ethmoid by fibrous tissue. Discrete jaw ligaments are lacking. When the lower jaw is depressed the premaxillae and maxillae rotate about the front of the ethmoid until the distal arm of the premaxilla is vertical. This only allows the jaws to open to a little over 20°. The feeding habits have become modified and are described in the appendix.

The adductor muscles to the lower jaw are small, and are shown diagramatically in fig. 13. They comprise a lateral and a medial muscle. At their insertion they are approximately equal in cross sectional area but before the posterior end of the sesa-moid articular the medial muscle has greatly increased in thickness and effectively surrounds that bone. Still further back a band of muscles from the quadrate to apparently the anterior of the operculum separates the medial and lateral adductor muscles. The lateral adductor muscle originates on the hyomandibular. Just anterior to the point of separation of the medial and lateral components the thick medial muscles split into a dorsal and a ventral portion. The dorsal portion origin-ates on the braincase and the ventral portion on the hyomandibular and possibly on the metapterygoid.

I am not certain of the identity of these muscles, and the terms applied to them are used purely descriptively.

2. Swimbladder

The swimbladder is simple and physoclistous. A gas gland and an oval are present.

DISCUSSION

The systematic position of *Indostomus paradoxus*

Indostomus is a bizarre, highly modified fish. Two major factors have combined to obscure its relationships; firstly the great elongation of the lower jaw and secondly the presence of dermal body armour.

The fish fauna of Lake Indawgyi has been listed by Prashad and Mukerji (1929) and does not contain any obvious relatives of this endemic species, so its peculiarities may be due to long isolation in the one lake basin. Prashad and Mukerji put forward the suggestion that the ancestors of *Indostomus* were not fresh water fishes, for in the early Tertiary the Bay of Bengal extended as far as Lake Indawgyi, and some marine fish could have been isolated and confined to the lake when the sea receded, this seems to be the most likely suggestion.

Prashad and Mukerji thought that *Indostomus* was " closely allied to the family Solenostomidae and to a certain extent the Syngnathidae of the order Solenichthyes Regan ". However they pointed out that there were certain differences between the three families. The structures described in this paper show that *Indostomus* is distant from the Syngnathidae and the Solenostomidae. The anatomy of the families comprising the order Gasterosteiformes (*senu.* Greenwood *et alii* 1966) will be described in subsequent papers, but for the moment Jungersen (1910) gives a good account.

Many of the similarities between *Indostomus* and the syngnathids are superficial and due to the presence of the annular armour and an elongated snout. The Syngnathidae and the Solenostomidae both show the following features of taxonomic significance which are not possessed by *Indostomus*.

1. Enlargement and/or complex articulation of the anterior 3 or 4 vertebrae with each other.

2. Sutural contact between the basioccipital and the autopterotic.

3. Separate ecto- and endopterygoids.

4. A metapterygoid which does not ossify as a separate bone but forms the metapterygoid process at the anterodorsal corner of the quadrate.

5. A dorsal lamina on the symplectic.

6. 4 pectoral pterygials.

7. No more than 3 branchiostegal rays.

These characters are enough to suggest that *Indostomus* and the syngnathids are not closely related, or at least should not be placed in the same order.

Bolin (1936) thought that *Indostomus* was closer to the Aulorhynchidae and the Aulostomidae than to the Syngnathidae and Solenostomidae. I hope to show in subsequent papers that the Aulostomidae are closely related to the Syngnathidae and Solenostomidae whilst the Aulorhynchidae is a family of moderately generalized fishes from which the Gasterosteidae are specialized descendants.

The Aulorhynchidae is the most primitive family of the suborder gasterosteoidei in which Greenwood *et alii* (1966) have placed *Indostomus*.   Although *Aulorhynchus* and *Gasterosteus* have several features in common and are clearly related there are several reasons why *Aulorhynchus* and *Indostomus* are most unlikely to be related. The trends in the aulorhynchid—gasterosteid lineage have not developed in a direction likely to produce indostomid facies.

Bolin (1936) admitted that the similarities he saw between *Indostomus* and *Aulorhynchus* were superficial, and this is so, but there is one surprising feature that they both possess and that is an elongated mandible.   It is relatively much shorter in *Aulorhynchus* than in *Indostomus* but even so it is produced backwards relative to the upper jaw further than in most fishes.

Certain other fishes eg. *Exocoetus volitans* (*Halocypselus* of Gregory fig. 101), *Parachaenichthys* (Chaenichthyidae), Gregory 1933) show the same phenomenon so perhaps one should not place too much weight on this character.

Indostomus and *Aulorhynchus* have few features in common, but because the former is more specialized than the latter many characters of the more primitive fish could have given rise to characters of the more specialized fish.   But none of the important features peculiar to *Aulorhynchus* and the gasterosteids are found in *Indostomus*.

Aulorhynchus in particular and the gasterosteids generally have the following characters not possessed by *Indostomus*.

1. Ascending processes on the premaxillae
2. Nasal bones
3. A well formed vomer bone
4. A triradiate " pterygoid " bone
5. Autopalatines
6. An infraorbital series of 5 bones in *Aulorhynchus*, 3 in the gasterosteids
7. Ascending processes on the parasphenoid which contact the frontals
8. An intercalar bone
9. Parietal bones
10. Upper pharyngeal teeth plates consisting of a UP2 and a fused UP3 & 4.   In *Indostomus* the anterior element is the larger and may be a fused UP2 & 3, with a separate UP4
11. 4 pectoral pterygials
12. Ribs
13. Pelvic fin skeleton
14. Dermal scutes along the lateral line, not full armour
15. Over thirty vertebrae.

Although many of these differences are only to be expected when comparing a generalized fish with a specialized fish some have been retained by the specialized descendants of aulorhynchids and are not present in *Indostomus*.

Indostomus must therefore be removed from the order Gasterosteiformes as it now stands (Greenwood *et alii* 1966, p. 398).   The status of the remaining families in that order will be discussed in subsequent papers.

The next problem is to try and decide which of the higher taxa of Rosen and

Patterson's (1969) modification of Greenwood *et alii* (1966) can best accommodate *Indostomus*. Only the superorders Acanthopterygii and Paracanthopterygii need be considered.

Rosen and Patterson (1969) have included the Atherinomorpha of Greenwood *et alii* (1966) as a series within the Acanthopterygii parallel to the berycoid—percoid lineage. There are certain features of the Atheriniformes which are shared to various extents with *Indostomus*. This does not necessarily imply that *Indostomus* ought to be placed in this order, but rather than it is of a similar level of complexity. This is almost stating the obvious for Rosen (1964) concluded that the Atherinomorpha arose from a group that stood somewhere in the ancestry of the Perciformes, and it is in this zone above the Protacanthopterygii and below the Perciformes that *Indostomus* must lie. The upper limit is set by Gosline (1966) who states that no percoid fish nor percoid derivative has nodules between the pelvic fin rays and the pelvic skeleton, which must therefore place *Indostomus* below the percoids.

Fishes in the series Atherinomorpha typically have a caudal fin skeleton which originates on one supporting centrum (as is the case in the majority of the Acanthopterygii). The caudal skeleton of *Indostomus* conforms to this pattern although the separate hypurals have fused up into one plate. This is possibly only to be expected because of the minuteness of its caudal skeleton.

There are some interesting trends within the suspensoria of some of the Atherinomorph families which may throw some light on the origin of the peculiar suspensorium of *Indostomus*. In the family Isonidae (Rosen, 1964) the autopalatine is greatly reduced and the endopterygoid is absent. This reduction in size and number of suspensorial bones has been continued further in *Indostomus*. The suspensorium and the jaws of the family Adrianichthyidae are of some interest. In many species of atheriniform fishes the upper jaw is protractile, but not in the Adrianichthyidae. There the maxilla is firmly joined to the upper edge of the premaxilla. The ethmoid is very large and has lost the disc-like appearance found in most atheriniforms. In these two respects it offers a parallel with *Indostomus*. The resemblance could go even further. In the adrianichthyids the lower jaw is of normal length and only the autopalatine links the upper jaw with the quadrate. If the proportions of the jaws and snout were altered to the proportions of those of *Indostomus*, a suspensorium very like that of *Indostomus* would result. This is pure hypothesis, but the adrianichthyids are a group of fish which satisfy the likely conditions for the pre-indostomid suspensorium.

If the lower jaw were elongated to articulate behind the eye, the autopalatine is already in position to elongate whilst keeping the upper jaw and quadrate tied together. As the quadrate is now behind the orbit and the lower jaw articulation almost vertical, there is no room for a large endopterygoid which could well disappear leaving just the hyomandibular, quadrate and symplectic to form the vertical column between the lower jaw and the braincase. The suspensorium of *Xenopoecilus* does not fit exactly into the appropriate pattern because the metapterygoid is now absent, yet is present in *Indostomus*, and although I have referred to the large suspensorial bone in *Indostomus* as the " pterygoid ", it could possibly be the autopalatine.

So, within the Atheriniformes there exist possible plans from which some of the characters of *Indostomus* could have evolved. It must, though be borne in mind that it is highly unlikely that the Adrianichthyidae have the basal suspensorial pattern of the order, and also that convergence could play a large part in the production of peculiarly modified suspensoria for somewhat similar jaws.

Parenthetically, it must be mentioned that the suspensorium of the ammodytoid *Hypoptychus dybowskii* (Gosline, 1963) is not unlike that of *Indostomus*. It differs mainly in having both the ectopterygoid and the palatine forming the lath in front of the quadrate and in the presence of a normal palato-maxillary connection. The jaws of *Hypoptychus* are approximately equal in length which suggests that this unusual pattern of suspensorium is not obviously related to the disposition of the snout and jaws and may well have occurred independently within the neoteleostei.

The Atheriniformes have the following features which differ from those in *Indostomus*.

1. A much higher number of vertebrae
2. No dorsal spines, and rarely a spiny first dorsal fin
3. Pelvic girdles with a long lateral spur
4. No trace of bony armour
5. Four pectoral pterygials, recessed within the scapulo-coracoid margin
6. Nasal bones usually present
7. A different arrangement of the upper pharyngeal tooth plates
8. Unarmed opercular bones

This makes the inclusion of *Indostomus* within the atherinomorph series unlikely. Little is known about atherinomorph ancestors, but the group evolved in the freshwaters of Asia, the area in which *Indostomus* now lives.

It is now necessary to try and fit *Indostomus* into the lower reaches of the Percomorpha series of the Acanthopterygii.

The order Lampridiformes contains the remarkable fish *Stylophorous chordatus* whose anatomy was described by Regan (1924). The most significant feature is the long mandible which in elongating backwards has carried the quadrate to a position behind the hyomandibular so that the suspensorium is angled forwards. The hyomandibular, quadrate and symplectic form a narrow column which is angled the opposite way from that in *Indostomus*. In *Stylophorous* the ecto-, endo- and metapterygoid bones are reduced to splinters between the quadrate and the hyomandibular. The autopalatine is a rod-like bone in a normal position but distant from the pterygoids. The premaxillae have large ascending processes and the mouth is highly protrusile. This elongated mandible is not universal amongst the Lampridiformes, but the modifications of the suspensorium form an interesting comparison with the situation in *Indostomus*. The presence of a basisphenoid, an orbitosphenoid, parietals, the dermopterotic-frontal contact which excludes the dermosphenotic from the skull roof, the high vertebral number long based dorsal fins without true spines and the absence of dermal armour are some of the many features which do not suggest any close relationships between the Lampridiformes and *Indostomus*. It is however, worth noting that three pectoral pterygials are common in that order.

Indostomus is far too specialized to be associated with the Beryciformes and their

early offshoot the Zeiformes (Patterson 1964). Any relationship with the Synbranchiformes and Channiformes can be dismissed.

The order Scorpaeniformes is suspected by Greenwood *et alii* (1966) of being polyphyletic, but typically these fishes have the second suborbital bone contacting the preoperculum and a caudal skeleton consisting of two plate-like hypurals sutured to the terminal half centrum. The family Agonidae contains armoured forms which have retained the ribs and an unmodified caudal skeleton. Despite the precedent in the dermal armour of the Agonidae, the Scorpaeniformes are a fairly well defined order which, if any stock underwent reduction would be unlikely to produce the indostomid facies.

This leaves two small orders to consider, the Dactylopteriformes and the Pegasiformes.

The only point of similarity between the Dactylopteriformes and *Indostomus* is that both possess a low number of vertebrae, 22 in the former and usually 21 in the latter. The osteology is otherwise substantially dissimilar (Allis 1909).

The Pegasiformes are as much a problem as is *Indostomus*. *Pegasus* has never been described in detail, Jungersen (1914) has only given a brief account of the fish and from this one may gather that *Pegasus* is, like *Indostomus*, in an apparently isolated position.

The Paracanthopterygii is a superorder of fishes which, in the words of its definers, Greenwood *et alii* (1966) " represents a spiny finned radiation more or less comparable morphologically with that of the superorder Acanthopterygii ". Rosen and Patterson (1969) have shown that many of the acanthopterygian features of the Paracanthopterygii are lost during the evolution of the superorder.

The majority of the species included in the five component orders are marine, but the most primitive order the Percopsiformes is now confined to the fresh waters of the new world. Rosen and Patterson (1969) have shown that the superorder is monophyletic but contains two lineages : the percopsid-gadid lineage and the batrachoid-lophiid-gobiesocid lineage. The most trenchant characters separating the Paracanthopterygii from the Acanthopterygii are the presence of a levator maxillae superioris muscle and a second free ural centrum in the caudal fin skeleton. During the evolution of the batrachoid-gobiesocid lineage these two characters were modified and are absent in the gobiesocids, nevertheless a multitude of less trenchant characters links the batrachoids to the gobiesocids.

The Gobiesociformes are highly specialized fishes, as is *Indostomus*, and comparison of the characters of *Indostomus* with the trends within the batrachoid line that produced the gobiesocid facies reveals a number of similarities. Many of these can be explained by convergence and parallelism, some characters are of much less significance than others but whether convergence and/or parallelism can explain the particular combinations of characters present in both is something that will have to be argued when our knowledge increases.

Characters and trends present in the batrachoid lineage and in *Indostomus* are
  1. Flattened skull roof
  2. Fusion of parietals with epiotics
  3. Autosphenotics flare forward

4. Absence of an intercalar
5. Horizontal alignment of the occipital condyles
6. Infraorbital series reduced to the lachrymal which lacks a suborbital shelf
7. Reduction of the pterygoid series
8. Hyomandibular and preopercular in intimate contact
9. Upper hypohyal elongated and lying over the cerataohyal
10. Six branchiostegal rays
11. Upper end of preopercular well below hyomandibular head
12. Posterior margin of opercular excavated
13. Caudal skeleton (in gobiesocids) fused up without a free parhypural
14. Pectoral radials enlarged
15. Coracoid with a posteroventral process
16. Spinous anterior dorsal fin rays
17. Rounded caudal fin
18. Scales absent
19. No orbito- or basisphenoids
20. Subopercular slender and directed towards the upper corner of the opercular
21. Adductor arcus palatini across the floor of the orbit
22. Pelvic fins subthoracic and with reduced number of rays
23. Upper and lower jaw teeth fail to occlude completely.

Some of these characters need further qualification. 1, 5, 12 and probably 8, all seem to be related to the flattening of the skull. Rosen and Patterson (1969) pointed out that in paracanthopterygians the exoccipital condyles tend to lie alongside the basioccipital condyle, whereas in the acanthopterygians they tend to lie above the basioccipital condyle. This is mechanically necessary in fishes which raise their heads, a practice found in both *Indostomus* and the paracanthopterygians. In the Scopraeniformes *Hoplichthys langsdorfii* the exocciptal flanges are level with the basi-occipital condyle ; in *Platycephalus insidiator* and *P. japonicus* they are only a little higher, and fail to meet medially above the basioccipital condyle. A similar situation is found in the perciformes *Gymnodraco acuticeps* and *Parachaenichthys georginaus*.

Number 13, the fused caudal skeleton, is another character which needs some comment. A caudal skeleton which has had all its components parts fused into a single hypural plate supported on one centrum is found in advanced perciforms as well as in the Paracanthopterygii and the Gasterosteiformes. In the case of *Indostomus* the evidence afforded by the second pre-ural neural spine (Patterson, 1968, Rosen and Patterson, 1969) cannot be called upon, because the neural arches of all the caudal vertebrae of *Indostomus* have fused with the dermal scutes. Most perciforms in which the caudal skeleton is fused typically have an autogenous parhypural whilst in the Gobiesociformes the parhypural is fused with the hypural plate. In the scombrids, where the parhypural is in some species fused with the hypural plate, a well developed parhypural process is evident. In the Gasterosteiformes (with the exception of the highly reduced caudal skeletons of the Syngnathidae) the parhy-pural, when fused, is usually obvious in alizarin preparations. The absence of an autogenous parhypural in *Indostomus* suggests a real affinity with the Gobiesocids, because although the caudal skeleton is as fused as it is in the syngnathids, the

caudal fin plays a much greater role in the locomotion of the fish. In other words the consolidation of the urophore elements is more likely to be the result of a phyletic trend (as in the batrachoid-gobesocid line) than of reduction resulting from a trend to develop a prehensile tail and lose the caudal fin as in the Syngnathidae.

The excavated hind margin of the opercular (12), is a feature that is also present in the Scorpaeniformes (a group that seems to have several paracanthopterygian trends) but the very spiny type of opercular present in *Indostomus* and batrachoids like *Opsanus tau* (with the consequent excavations of the rear margin) does not seem to be repeated anywhere else in quite this form. None of the batrachoids have as many pungent spines as does *Indostomus*.

Characters 2, 4, 6, 7, 10, 13, 14, 16, 17, 18, 19, 20 and 23 are far from rare in the Acanthopterygians and their significance would seem to lie in their particular combination in one group of fishes.

Characters 3,9, 11, 15, 21 and 22 must indicate either that *Indostomus* has some affinity with the batrachoid lineage of the Paracanthoptergyii or that it exhibits a remarkable degree of convergence in these rather specialized features.

The jaws of *Indostomus* are highly aberrant but would seem to conform to the "maxillary rotation" style present in the higher Paracanthopterygii. Within the batrachoid lineage when the levator maxillae superioris muscles are absent, no muscles insert on the maxillae and the rotation of the upper jaw in under the sole control of the depression of the lower jaw.

One would expect that the peculiar ethmoideum of *Indostomus* would be too specialized to reveal any affinities with more orthodox fishes. The only points worth mentioning in this context are that in *Opsanus beta* the vomer is fused with the ethmoideum (Rosen and Patterson, 1969), and that in *Opsanus tau* at least (see fig. 263 in Gregory, 1933) the physical disposition of the ethmovomer block and the pterygoquadrate bars are much the same as they are in *Indostomus*.

Primitive Paracanthopterygian features present in *Indostomus* include the following :

1. Absence of a supra-temporal fossa
2. Two openings to the pars jugularis
3. Parasphenoid-pterosphenoid contact
4. No pelvic spine.

Apart from the specializations of the snout and jaws, there are several important differences between *Indostomus* and the paracanthopterygians. The following are characters of *Indostomus* which are not found in the more highly evolved paracanthopterygians (although some are present in the Percopsidae).

1. A strong ventral process of the posttemporal
2. Short hypobranchials
3. A distinct gap between the epibranchials 3 & 4
4. No reduction of the basibranchials
5. No ascending processes on the premaxillae
6. Considerable reduction of the lateral line system
7. Absence of ribs
8. Dermal armour.

It seems then that *Indostomus* contains a mosaic of a few features that are primitive to fishes of the level of basal paracanthopterygians, several features also found in members of the batrachoid-lophiid-gobiesocid lineage and a few characters *sui generis*. The presence of the characters peculiar, in this combination, to the batrachoid-gobiesocid lineage make it less likely (but not impossible) that a similar combination could be found in acanthopterygian fishes.

The balance of evidence suggests that *Indostomus* could have evolved from one of two species. It could have evolved from a species just on the paracanthopterygian side of the paracanthopterygian-acanthopterygian dichotomy and then have evolved along a line somewhat parallel to the batrachoid-gobiesocid line to produce a fish with the short dorsal and anal fins and the few rayed caudal fins as in the Gobiesociformes. The other possibility is that *Indostomus* evolved from a species somewhere on the line leading to the gobiesocids. The fact that the most precise characters are those shared with the more highly evolved paracanthopterygians is some evidence for this.[1] The fact that the gobiesocids are marine littoral forms found in the Indian Ocean does not contradict this when Prashad's and Mukerji's views on the origin of Lake Indawgyi are taken into account. The presence of the primitive features could then, in some cases be explained by secondary reduction and simplification.

Much of this discussion is, of necessity, speculative, but the balance of evidence leads me to consider *Indostomus paradoxus* to be the only species of a new Paracanthopterygian order ; order Indostomiformes, which shows some affinities with the Batrachoidiform-Gobiesociform lineage of that superorder.

The diagnosis of the order Indostomiformes is essentially that of the species viz. small freshwater fishes from Upper Burma, the body has a complete dermal armour covering ; the head is depressed and is mobile ; the pterygoid series of bones is reduced in number ; the upper jaw is not protrusile ; the lower jaw is long ; a series of isolated spines is present in front of the dorsal fin; the dorsal and anal fins are short based and opposite each other ; the pelvic fin contains fin rays with cartilaginous nodules at their bases ; there is no pelvic fin spine.

SUMMARY

1. The anatomy of *Indostomus paradoxus* is described.
2. A new order-INDOSTOMIFORMES is proposed to contain this single species.
3. It is suggested that the order Indostomiformes be placed within the superorder Paracanthopterygii and probably near the Gobiesociformes.

ACKNOWLEDGEMENTS

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[1] Whilst in the realms of speculation I am tempted to compare the behaviour of captive *Indostomus* in leaping out of the water and sticking onto the glass (presumably by a combination of surface tension and a flattened belly—see Appendix) with the trend to develop a sucking disc in the Gobiesociformes.

in putting this work on paper in an orderly fashion and eliminating many of my mistakes. Needless to say any remaining errors are all my own work.

To all these people I gratefully offer my thanks.

APPENDIX I

Based on notes made on the behaviour of the living *Indostomus* by Dr. Alan Tubb

Notes on *Indostomus*

About 140 specimens collected from a small creek entering the west side of Lake Indawgyi were brought alive to Rangoon and installed in two small (10 gallon) aquaria, on 3 April 1956.

One aquarium tank contained a pure stock of *Indostomus*, about 110 individuals, the other contained a variety of small *Barbus* spp., *Platypoecilus* and *Xiphophorus* hybrids.

Both tanks had sand on the bottom and were planted with clumps of *Cabomba* and dwarf *Sagittaria*.

In the community tank, the older inhabitants spent some time chasing and nipping at the *Indostomus*, without however doing any obvious damage, and after two days the enlarged community settled down and no further attacks occurred.

The *Indostomus* is quiet in behaviour, and generally slow-moving. Normal movement is effected almost wholly by means of the pectoral fins which maintain a constant rapid fluttering movement, even when the fin is apparently completely at rest. When alarmed, these fish move with remarkable speed, apparently using the relatively large fanshaped caudal fin. The dorsal and anal fins are usually folded along the body, but may be fully spread when the fish is moving slowly, with no apparent purpose, or when resting in an inclined position close to an ascending strand of vegetation. The dorsal and anal fins, together with the tiny pelvics are used as " brakes " and are widely spread to retard forward motion. They and the caudal fin are often spread when the fish is "hanging " in the water, presumably to provide an increased resisting surface.

The *Indostomus* appears to feed entirely on animal food, but will only take live organisms. In the aquarium, they fed readily on small tubificid worms which were scattered over the surface of the water and allowed to sink slowly to the bottom. Only rarely were worms actually sinking taken by the fish. In almost all cases, the worms fell to the bottom and were then taken.

When approaching a food item, the *Indostomus* moves very slowly, all fins depressed except the pectorals, which maintain their constant fluttering motion. When close to the food organism, the fish rolls gently over to one side, either right or left. In the case of a worm protruding from the sand, the roll may be sufficient to place the transverse axis of the body at 90° to normal. The final millimetre of movement is accomplished by a sudden dart (the jaws are not protrusible) and the food item snapped up. If the worm is deeply imbedded in the sand, the fish, having gripped the exposed portion, wriggles violently backwards, and usually succeeds in withdrawing the worm from its tube.

Colonial protozoans growing on the aquarium walls or on the vegetation are taken in a similar manner, the degree of rolling depending on the situation of the colony. In this latter case, the withdrawal by the fish is steady, and usually only a few millimetres.

Normally there appears to be little belligerence between individuals, although actual shoaling does not occur, each fish moving independently of other members of the community. Occasionally, however, a fish seems to establish a kind of temporary " territory ". These individuals, by their more slender form, and the absence of the whitish or greenish mass visible through the translucent walls of the abdomen of other less slender specimens, are probably males.

In the cases observed, the " territory ", which does not appear to exceed in diameter twice the total length of the fish, is maintained only for brief periods, rarely more than 15 minutes, but during this time, all other members of the species which infringe the boundary are driven off, although no damage appears to happen to the invader.

Despite its dermal armature, the fish is surprisingly flexible in life, and can bend in an almost complete circle, the snout approaching within a few millimetres of the caudal fin. The most remarkable feature, however, is the flexibility of the " neck ". It is one of very few fishes known to the writer, which can actually " raise its head ". The free anterior vertebrae, permit a vertical flexure of the head to an angle of about 10° from the main axis of the body. Lateral and ventral flexures of about the same order of magnitude also occur.

In the tank containing only *Indostomus* the fish showed a strong tendency to assemble in the darkened areas, particularly, a number would cluster, heads upward, on the inner surface of the angles of the tank, where they were sheltered from the direct front lighting. Not all followed this habit, many spending the great part of the day lying flat on the bottom, or resting head upwards at an angle of 30–75° among the vegetation. These resting periods appeared to be prolonged, although it was not possible to be sure that any one individual remained in the same place for an extended period.

A peculiar reaction was noted when the fish were unusually disturbed, either when the glass of the tank was being cleaned, or occasionally when the " mulm " was being siphoned from the bottom. Most of the fish would dart wildly about, producing a noticeable clicking sound as their bony snouts bumped against the glass walls of the tank. A few, however, would leap clear of the surface and adhere to the upper part of the glass, 1 or 2 centimetres above the water. They failed to respond to a gentle touch, remaining quite immobile, and either had to be gently pushed back into the water, or allowed to remain until they flipped back again of their own accord. One specimen was observed to remain sticking to the glass for $4\frac{1}{2}$ minutes before wriggling into the water again. They apparently suffered no damage from this exposure.

In the community tank, the *Indostomus* paid little attention to the other species, simply moving slowly aside as another fish approached. The current induced by the sudden sweep of the caudal fin of a larger fish often tumbled these extremely light creatures over and over, but did not appear to cause them a great deal of alarm.

The respiratory movements are worthy of note. The mouth remains open constantly, except when food is actually being ingested, and the gill covers are spread outwards, forming a narrow frill one each side of the head. The gills are thus partly exposed and are clearly visible from any position behind to the posterior edge of the gill covers, or from below, the branchiostegals and their connecting membranes also being widely spread. There is a steady rapid pulsation of the isthmus and connected membranes, but as there does not appear to be any inner postlabial skin fold to serve as an oral valve, such as that found in certain of the siluroids and other fishes, it is difficult to avoid the impression that the respiratory current is not, in part at least, induced by the continuous fluttering of the pectoral fins. When " stalking " its food, the *Indostomus* depresses the otherwise extended opercles and branchiostegals and the pulsation of the isthmus appears to cease entirely.

The breeding of this fish has not yet been observed, but several specimens, apparently females, showed evidence of gonadal development during late June 1956. These fish became markedly more robust in appearance and, through the translucent body walls, the development of the ovaries was readily observable. The first obvious stage was the appearance of a pale creamy mass occupying about half the length and about one third of the volume of the abdominal cavity, extending from opposite the first dorsal spine to the vent. In some of the fish under observation, this mass later assumed a delicate jade green color, and although the length did not appear to increase, the distension of the abdomen became more marked. In the noticeably more slender specimens, and particularly in those showing the temporary " territory " habit mentioned above, no such evidence or gonadal development was observed.

When captured, all specimens were generally dark to dusky brown the fins showing the transverse banding mentioned by Prashad and Mukerji (loc. cit. p. 221). In the aquarium tanks however, in the clear water and under the relatively bright light conditions, most specimens rapidly became a very light, honeybrown color and the fin patterns were reduced to extinction. Dorsally, on each side of and close to the mid line were four bright golden squares, situated at the interspaces between the dorsal spines, i.e. on the 4–7 rings. Some specimens occasionally become somewhat darker in color, when indistinct transverse bands of cloudy black appear, apparently coinciding with the rings and extending from the anterior (scapular of Prashad and Mukerji) to the first caudal ring. On such individuals, the transverse banding of the fins, particularly the caudal fin, becomes evident.

KEY TO FIGURES

an	angular	mpt	metapterygoid
anf	anterior nostril	mx	maxilla
ar	articular	na	neural arch
bb	basibranchial	op	operculum
bo	basioccipital	pmx	premaxilla
bp	body plate	pnf	posterior nostril
br	branchiostegal ray	pop	preopercular
c	centrum	pro	prootic
cb	ceratobranchial	ps	parasphenoid

ch	ceratohyal	pt	pterotic
cl	cleithrum	ptm	posttemporal
co	coracoid	pts	pterosphenoid
d	dentary	pty	pterygoid
dpt	dermal part of pteroticum	q	quadrate
dsp	dermal part of sphenoticum	r	pectoral pterygial
Dsp	dorsal spine	sa	sesamoid articular
e	ethmoid	sc	scapular
eb	epibranchial	scp	scapular foramen
eh	epihyal	scl	supracleithrum
epo	epiotic	se	supraethmoid
ex	exoccipital	so	supraoccipital
f	frontal	sop	suboperculum
hb	hypobranchial	sp	sphenotic
hm	hyomandibular	sy	symplectic
hy	hypural	tp	transverse process
ih	interhyal	tpf	facet on transverse process
iop	interoperculum	uh	upper hypohyal
la	lachrymal	up	upper pharyngeal
le	lateral ethmoid	ur	urohyal
lh	lower hypohyal	v	vertebra
lig	ligament	vo	vomer
llc	lateral line canal		

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